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MONOCARPY AND PSEUDOMONOCARPY IN THE CYCADEOIDS

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Seed plants which fruit once only in the normal lifetime, and then die down to make way for the new set, are described as monocarpic. The habit is of much interest to students of ecology and succession.

As ordinarily used, monocarpy is a rather fixed term which requires some extension, or even redefinition. In a stricter sense, the field of rye is monocarpic; though the usage is far less definite in its common application to plants much longer lived than annuals or biennials. There would, however, be a double reason for not calling a "bracken fern" monocarpic; since after the fertile frond bears its *spores*, the root-stock grows on, propagation being only secondarily dependent on either the sexual or the asexual generation. And somewhat similarly, any seed plant which, after the wilting down of a fertile stalk of one or more seasons, renews its growth from the root, is falsely monocarpic. It is an inadvertence on the part of botanists to cite the "century plant" as truly monocarpic, or any plant which does not fixedly persist by reseeding, or solely so persist.

There appear to be some basic physiologic distinctions or phases in monocarpy. The Agave (or *Yucca filamentosa*, which regularly sends up the new buds, with very little germination of seed) does store the materials for the fertile shoot. But in such plants the length of the vegetative phase may be variable, or doubtless even local and individual. Besides, wherever the basal buds grow forward, there is some analogy to the fertile axis of limited growth in trees.

The production of flowers or fruits usually means the growth of peduncular tracheidal or other structures old in the history of the plant, supplying greatly modified or reduced sporophylls; so that fruit maturity may mean, not merely exhaustion of the parent stem, but a heavy scar or injury to the stem not easily survived. Thus as a plant is modified from age to age, and the gap between fruit and vegetative structures widens, proliferation of the fertile axis may become difficult or quite impossible. And such has in fact become the condition in the vast majority of seed plants with renewed growth from the base of flower or cone. Particularly in the conifers the occasional appearance of proliferate cones may be regarded as reminiscent of a time when there were some normally proliferate types in the ancestral series.

Contrariwise, the budding power of stems divested of their foliage or cut down to the base, is often striking in the extreme, especially in some of the Pandanales because little expected. Renewed growth from stem-base or root may then be a characteristic of singular or extreme types. It may even accompany gigantism.

Undoubtedly there is a less known side to monocarpy and the monocarpic tendency; while even in the commoner instances, variations either individual or within the habitat, and details concerning any subsequent root branching, may fail. The classical example is of course the "umbrella palm" of Ceylon, *Corypha umbraculifera*. After a vegetative period of towards forty years the mature height of sixty feet is reached, when in a single short season the stem shoots forty feet higher as a much branched flowering stalk. Meanwhile the foliage fronds wilt down and leave this immense terminal inflorescence with a branch spread of thirty feet, bearing tens of thousands of flowers.[1]

This unparalleled gigantism, however, scarcely exceeds in outright interest a Jamaica plant known as the "pride of the mountain," *Spathelia simplex*, a member of the rue family. For this plant is nearly related to hardwood perennials like Citrus, and the Rutaceæ are not so generally monocarpic. The slender trunk, scarred by the fallen leaves, reaches a height of fifty feet, bearing an apical cluster of large, velvety, pinnate leaves three or four feet long. The pinnules are numerous (45–81), sessile, oblong-lanceolate, crenate. At maturity a large terminal panicle of showy purple flowers rises above the leaves, the plant dying down after the ripening of fruit. There is thus afforded an example of a tall and quite typical dicotyl of much the same habit and habitus as the "umbrella palm."

The primary form of monocarpy finds a notable variation along ecologic lines in the greatest of the grasses, the bamboos. The life cycle in the bamboos varies greatly. Many species bloom annually; and there are also cases of sporadic flowering, with, however, the final production of flowers on all the culms—ripening of seed then terminating the life of the plant (*Arundinaria Simoni*). In the bamboos of the south Brazilian provinces of Santa Catarina and Rio Grande do Sul, along the borders of the imposing *Araucaria brasiliana* forest, a thirteen-year monocarpic period occurs. For *Bambusa tesselata* in cultivation a not very authentic record of a sixty-year cycle is given.

Floral periodicity is well attested in the Indian (Ganges) *Bambusa arundinacea*, reported in flower in the years 1804, 1836, 1868, [1900]. In the Blue mountains of the Island of Jamaica at an altitude of 4,000 to 7,000 feet over a region ten miles long, occurs the "climbing bamboo" (*Chusquea*

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[1] All the genus Corypha is perhaps more truly monocarpic than are other so-called instances. Root shoots are not sent up. There are two Ceylon species, and other representatives in Bengal and farther eastward. In this connection there should be added the interesting case of the Mauritius hemp, *Furcraea americana*, an agave-like plant. Suckers are not readily produced, but any such flower at the same time as the parent stock. Propagation is mainly by bulbils after flowering.

abietifolia). Here, extending over more than a year in 1885–6, flowering and dying down were general; this occurred again in 1919, when 98 percent of the plants formed the dead entanglements, and the young plants 18 inches high covered the ground in long stretches (as recently described in this Journal).[2] A rough thirty-three-year period is indicated, with only minor or suppressed seasonal factors.

These are communal forms, and whoever has seen one of the isolated dead pure stand thickets of bamboo in an open hilly region, as in parts of southern Mexico (Oaxaca), where there is a long, dry winter period, understands that average length of life and single flowering are complementary, intensified habits. In such plant communities the life of the individual is simple, set, and tense; and as soon as a considerable number of the plants fruit and die down, the light, heat, moisture, and soil conditions of the copse change rapidly. Only the plant behaving in the average way tends to leave its progeny. Even in the tropics there are forms which flower over wide areas on precisely the same day. Then, in the forests of Pegu, certain orchids are seen to blossom as the limbs on which they are seated lose their leaves. Yet there is the remarkable variation in that some trees bloom quite through the year, as the mango, silk cotton, and fig. This has been noted especially in orchids.

Casually, this much may be said of the monocarpic habit. Plants seemingly take full advantage of their environment in reaching their many forms. But they grow as they may, and reproduce as they must. The law is simple, complex though its expression may appear. Reproduction is sharply seasonal in the severe environment, and of more varied phase in the soft climate where growth factors find their favorable mean. In the cool temperate zones, the period of flowering varies for weeks as moisture and heat vary with the unusual season. In the tropics the utmost variations are found. Many of the woody plants are not dependent on their foliage in blossoming in or after the dry season. Such is the habit of various magnolias of the subtropics, and further north, where the burst of flowers is put forth earlier than the young leaves easily grow. These are tender and in our climate whipped by chill winds of early spring. Yet other trees are, as Schimper notes, evergreen in their flowerless youth, losing their foliage as they flower and fruit. Though such (*Schizolobium giganteum* of Java) suggest a certain advance toward monocarpy.

Evidence of Monocarpic Conditions in Cycadeoids

In few extinct plants could we hope to detect evidence for so recondite a feature as flower growth but once in a lifetime, or for any modified form of monocarpy—not even under most favorable circumstances of fossilization. Among all the plants of the past, the petrified cycadeoids alone present the evidence for monocarpic tendencies and pseudo-monocarpy in the numberless fruits, from the youngest stages of growth to the mature seed cones held securely packed between the leaf bases forming the heavy protecting outer "armor" of the short, robust trunks (note Plate IX).

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[2] Seifriz, William. The length of the life cycle of a climbing bamboo. A striking case of sexual periodicity in *Chusquea abietifolia* Griseb.
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It was first observed in studying the petrified stems from the Black Hills that a tendency to monocarpy was present. In fact, this was considered fairly proven in those instances in which the imbedded young axillary fruits were found throughout the armor. Thus far five of the species of Cycadeoidea are viewed as more or less completely monocarpic:

1. In the trunk fragment from northwest of the Grapevine Valley, Colusa County, California, the axils of the old leaf bases are regularly occupied by groups of robust bracts, few in number and apparently surrounding the ends of slender old peduncles. The trunk may of course have died down. (An illustration is given on Plate LXX of U. S. Geological Survey Monograph XLVIII; the type is in the U. S. National Museum. It is the *Cycadeoidea Stantoni*. Thin sections are not available.)

2. The type of *Cycadeoidea nigra* from Boulder, Colorado, is a trunk segment of considerable size from the mid-region of a columnar stem supposedly a meter high. Again each leaf-base axil is occupied by an old, rather slender peduncle bearing few and heavy bracts. Thin sections have been cut from the armor, and should be amplified. No basal parts of fruits have been observed; but as in the preceding instance the fruiting space appears occupied, and a final series is indicated. The flowers may have failed of conservation, or the stem may be old. This type is receiving further study. It belongs to the Colorado School of Mines, and full citations and description may be found in Wieland, *American Fossil Cycads*, volumes I and II (Carnegie Institution of Washington Publication 34).

3. *Cycadeoidea Masseiana*, a remarkably fine columnar trunk segment greatly resembling the foregoing, from the "scaly clays" of the flanks of the Apennines, and reposing in the Capellini Museum, Bologna. Thin sections regularly cut young, small fruit axes in the axils of the large, old leaf bases of the very heavy armor. Again the thin sections should be much amplified. But as even the lesser ones cut by both Capellini and myself show the fruits, it is certain these are very numerous, and quite uniformly young. A fine model of this specimen is in the Yale collection of study materials. (Further reference in *American Fossil Cycads*.)

4. *Cycadeoidea Fisherae*, which may be only some varietal form of the *Cycadeoidea marylandica*, from the Potomac formation of Maryland, exhibits a most remarkable series of very young axillary fruits. No sections have ever been cut from this specimen, the conservation being hardly equal to that of either the Italian or the Black Hills trunks; though it is certain that nearly all the way from base to apex there is a fruit of some form in the axil of each leaf. It is of course possible that two floral forms are present, one staminate, the other ovulate; and it may here be remarked that, with

the accumulation of detailed studies of exceptionally silicified trunks, many interesting features and variations of cycadeoid fructification can yet be brought to light.

5. The most remarkable petrified plant of any kind ever recovered is no doubt the National Museum specimen found by Dr. Darton on the eastern Black Hills "rim," and illustrated by some ten plates in volume II of *American Fossil Cycads* as *Cycadeoidea Dartoni.* The type consists in the upper half of a columnar trunk perhaps a meter tall, with a finely conserved terminal bud. The armor is literally packed with hundreds of mature cones, with the dicotyledonous seeds conserved in great numbers. There are very few old or aborted axes of any kind, and, while near the summit there are a few smaller and perchance younger fruits, the great series is uniformly mature. Some further sections from about the apex remain to be made. But it is to be cited that the old leaf bases appear desiccated or shrunken, while ample sections show no trace of a succeeding foliar crown; though a fine crown of young fronds surmounts a scattered growth of flower buds in the very different species *Cycadeoidea ingens*—a great type of six hundred pounds' weight from the Piedmont-Black Hawk locality some twenty miles due north of the point where the *C. Dartoni* was found. Yet other species could here be cited.

In view, then, of comparable species with the full series of lateral axial fruits immature, as in *C. Masseiana* and *C. Fisherae*, and of further types with peduncle series, or with isolated fruits, the *Cycadeoidea Dartoni* appears monocarpic. Vegetative growth has apparently ceased in a time of culminant fructification with the emergence of all the axes the stem can ever produce. But it must be admitted that if only a small percentage of the apical fruits are found younger or less full grown than the greater lateral series, a partial monocarpy or pseudomonocarpy is indicated. Of this more, with extension of thin section series. The available series of large tandem sections is shown on Plates 46–50 of *American Fossil Cycads*, volume II, so that the reader may somewhat judge for himself. It may be added that the tandem sections of *C. Dartoni*, though not at any time regarded as complete without continuation to near the crown, traverse the trunk from the base of the recovered segment upward for 35 centimeters, cutting nearly fifty seed cones. And throughout this long distance a series of uniformly mature cones is present, and evidently extends near to the trunk summit. In the belt crossed by the sections there is an average superficial area of five to six square centimeters to the cone, indicating for this upper trunk segment not less than 500 cones with the ripe embryos. On the basal segment of the trunk, which was not recovered (and which I have twice sought for at the locality on Battle Creek), there were at the lowest estimate as many more, or 1,000 in all for the entire stem (Plate XI).

If a yearly cone production is concealed above, it had become small. Among so many cones, imperfectly grown examples are to be expected, and certainly a few of the topmost of the cones below the terminal bud appear greener and less mature. In one cone inserted 6 centimeters below the apex, the seed stem mass is split off from the receptacular cushion, with the lower portions of the stem bundles left behind adherent to the cushion, so that these bundles are seen to traverse the clear silica the full distance between the cushion and the seed stem mass. The seeds of this cone are not conserved, but the bundles show a somewhat similar tension or tearing out in occasional cones farther down in the series. In a smallish cone five centimeters below the terminal bud, the basal seed stem mass is again all that is conserved, but it appears mature. These two bases of cones may be seen in the photograph of the full longitudinal section of the entire trunk segment (Plate 43 of *American Fossil Cycads*, volume II).

Pseudomonocarpous Types

Apparently monocarpy is a phenomenon at present confined to the angiosperms. At least no characteristic instances now occur in the gnetaleans, and none in the conifers. The latter are no longer capable of annual or biennial fructification, as perchance in some remote period of their history. The dwarf or pygmic species are simply those of the high mountains, such being stubbornly coniferous and longevous.

It is therefore curious to find that there is in the cycadeoids a near approach and parallel to a kind of pseudomonocarpy found in several conifers of the California Sierras. The so-called "knob cone pine" (*Pinus attenuata*) occurs in much restricted "close willowy groves" of the dry slopes —in the San Bernardino range at about 3,000 feet, or along lower forest limits. It is lower and more abundant in the Shasta region. This pine varies greatly in size, from 30 meters high down to only two, though mature. (The wood is of low specific gravity, only 0.35.) At the age of seven or eight years the large cones begin to appear, borne close to the stem or larger branches, and there persist from year to year until the older series is quite imbedded in the bark. So indurated and resistant are the sporophylls in fact that often the seeds are not shed until the trees die, the groves being periodically fire swept. Then, the cones split open and reseed as if from a single crop, the trees in the "stands"always being of the same age.[3] A life-like picture of this singular pine is given by John Muir.

Also, *Pinus Coulteri*, as I noted in the San Bernardino range, bears while younger a certain resemblance to the "knob cone." The very large cones are then borne only on the excurrent stems, and the first cones may abort for some distance up the trunk, leaving near the summit only a few, or but

[3] It is evident that the cones near the base of an old tree reached maturity while the stem diameter was yet small, and that if they remained in the position where they first grew, they must become imbedded in the solid stem wood. But what happens is that the quite sessile cone is torn from its seat and carried outward by stem growth, with the bases deep set in the bark. The long persistence of the cones is partly due to an uncommonly hard resinous lacquer-like coating.

a single pair, of the mature cones about oppositely borne. The basal scales of the cones may be quite grown round by the bark. As the tree is destined to grow forward, there is of course nothing like an initial stage of true monocarpy in which apical growth must fail.

Obviously in those species of Cycadeoidea such as *C. dacotensis* and *C. Reichenbachiana*, with a very heavy armor and scattering fruit axes, there may have been retention of the mature cones for several seasons, closely packed in between the leaf bases and there kept dry and free from decay by an abundant drooping ramentum. But the cones themselves did not tend to persist intact after maturity, because the Araucaria-like grouping of the sporophylls allowed easy separation and splitting free of seed stem and interseminal scale alike; while a simulated monocarpy does not sufficiently explain the condition found in the several cycadeoid species above cited. In order, however, to reach certain main conclusions it is necessary briefly to bring to view the xerophyllous character of the heavy-stemmed cycads, their geographic range, and also the climatic factor.

Xerophyllous Features of the Cycadeoids

Two main series of the petrified cycadeoid stems occur in the western Cretaceous. The lower series is from the Morrison (Como of Marsh). At one point near the so-called "Bone Camp" in the Freeze Out Hills twenty miles northerly from Medicine Bow, Wyoming, the trunks have been found abundant in close association with the sauropod dinosaurs; but the cycad species again recur more scatteringly with the dinosaurs in the western Black Hills "rim." The stems are so beset by scaly ramentum that resemblance to an "old man cactus" was early suggested, as some evidence of growth in dry situations, although this idea is neither confirmed nor contradicted by the presence of a fairly primitive pine (?) which I lately found closely associated with the cycads of the "Bone Camp" (so named from the bones of the great dinosaurs there found). The wood of these early pinaceans is dense, the wood rays are small, and the growth rings are very pronounced. Evidently growth was sharply seasonal, summer and winter, or dry and wet.

The second and greater series of petrified trunks occurs in the succeeding Lakota of the Black Hills, with several hundred feet of sediments intervening. The horizon is considerably younger, and conifer stems are again conspicuously associated, though insufficiently studied. One is an Araucarian, called by Knowlton *Araucarioxylon Hoppertoniae.* Again the growth rings are pronounced.[4]

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[4] This wood offers a simple but strong structure contrast to that found with the cycadeoids in the Freeze Outs. That wood is less Araucaroid, although the stems are above spoken of as early Pinaceans or Abietineans, in only a broad or perhaps Jeffreyan sense. I do not find full identity with any described form, though a relation to Prepinus (Hollick and Jeffrey) may be indicated by an imbedded shoot with centripetal wood.

Whatever these conifers may mean, the cycads are in their entire organization highly xerophyllous. There is, first, the profuse scaly ramentum thickly investing the frond bases as far out as preserved, and found scant in only a few instances (*C. Stilwelli* of the Black Hills, and an undescribed form from a much higher horizon in Alberta). Also, as Dr. Stopes has very lately found in a young lateral leaf crown long since cut at the British Museum, the under surfaces of the pinnules bear densely packed hairs. The feature is present in the American leaf series but varies greatly in its development with the species, of which at least four with well defined hairy leaves are known. The dense packing of pinnule hairs in *Cycadeoidea ingens*, as faintly preserved, simulates a tissue, in some parts of the frond as thick as the folded pinnules, and ending in a clear, sharp chalcedony line. These hairs are well cutinized, and the reduced transpiring surface, taken with the latitude (44°), suggests a warm-temperate desert climate. That these features and facts were long overlooked is quite inexcusable, though partly explained by the intention to come back to the critical study and illustration of cycadeoid frond structure. The character may be expected in some of the Mesozoic imprints, and is in physiologic accord with the free growth of angular scaly tomentum borne by the cycadeoid microsporophylls as they form the domelike apex of the young flower buds.

The foliage crowns of five American species of cycadeoids are structurally known. These are in order of discovery: *Cycadeoidea ingens*, *Cycadella wyomingensis*, *Cycadeoidea colossalis*, *C. marshiana*, and *C. dartoni*. But many more trunks with crowns remain to section.

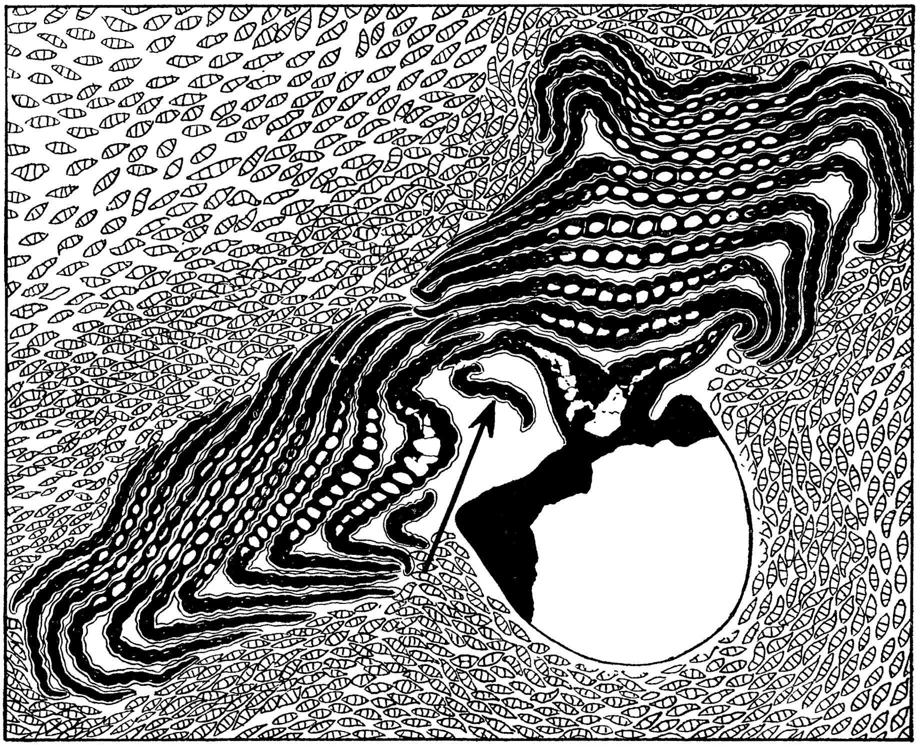
In general appearance the mature frond is absolutely determinate. The petiole was heavily clad in ramentum, varying considerably with the species, and becoming hairy instead of scaly about the insertion of the lowermost pinnules. Thence upward the upper surface of the rachis continues hairy with the hairy growth running out more or less freely all over the under surface of the pinnules; while the lower rachial surface and upper face of the pinnules remain smooth. (Note Plate XII, and text fig. 1; also Plate X, showing comparable Jurassic imprints.)

The picture, therefore, of the heavy-stemmed cycadeoids is a very well defined one of dry desert plants with all their parts, stem, fronds, and fruits beset by scales, hairs, or tomentum. And, moreover, a curious but deeply interesting bit of confirmatory geologic evidence is afforded by the presence in the Lakota of reefs of calcareous tufa accompanied by numerous polished pebbles, held to mark recedent lake shores of increasingly dry regions. Though it would be an error to view the cycadeoids as dependent on as

There are no resin canals, and no bars of Sanio or other modern features in either the tracheids or the rays. The radial tracheid pits are in one row, very rarely two, and never crowded or compressed. The rays are one to twenty cells high, normally ten, and one cell thick,—or two, for a distance of a cell or two.

It is probable that both these types of wood, Araucaroid and Pinoid or more Abietinoid, will yet be found occurring alike in both of the cycadeoid horizons.

distinctly tropic climates as present-day cycads. In accord with a world-wide distribution, a distribution exceeding that of cycads all the way from Florida to near the pole, the former had plasticity of both flower and leaf. Whether to be viewed as forerunners of the angiosperms or not, the capacity to live in varied climates must be hypothesized. It is not, however, likely that the Dakota cycadeoids, fringing as they did more or less pure-stand forests of pines and araucarians, could have endured as severe a climate as that of the Argentine "stands" of *Araucaria imbricata* facing the dry treeless country to the west of the Patagonia plateau in south latitude 35°–38°. But with the young leafy crowns so thickly beset by ramentum and the fruits so enclosed by bracts and the armor, there was full protection from many degrees of frost and from a time of snow.



TEXT FIG. 1. *Cycadeoidea Dartoni* (?). Young frond deeply imbedded in the petiolar ramentum. The arrow shows the basal ears as in Otozamites. The two ranks of folded pinnules face the trunk axis. Finer hairs and histologic structure not conserved. Transverse thin section × 30.

RANGE OF LARGE-STEMMED CYCADEOIDS

In North America, on the Atlantic-Gulf border, the evidence of an extended cycadeoid habitat is conclusive. Low down in the Potomac formation of Maryland in the Arundel (?) occurs the characteristic *Cycadeoidea marylandica* in latitude 39°. And twelve hundred miles to the southwest this same form recurs in Wise County, Texas, latitude 33°.[5]

About the same time the Arundel cycadeoids formed this southeastern continental fringe, a second and highly xerophyllous group of very small trunks finds a certain extension from the Freeze Out Hills of Wyoming to the Black Hills, or from latitude 42° to 44°.

As the greatest of all American occurrences, the cycadeoids of the succeeding Lakota girdle the Black Hills in latitude 43° to 45°, while two isolated finds, which may be nearly associated, extend this range on from Colorado to California on the 39th parallel, about 1,000 miles.

Correspondent to this greater North American extension, there is in Europe a triangle of occurrence with an apex in the Apennines in latitude 44°, and with a base of 1,000 miles from the Galician Carpathians and Cracow in latitude 50° to the Isle of Portland in latitude 51°. As in America, the north-south limits are only seven degrees apart. But high in the upper Cretaceous these limits are slightly extended. In the Upson Shales of Maverick County, Texas, occurs the isolated *Cycadeoidea Uddeni* in latitude 29°, while in the Belly River formation of Alberta, of nearly the same age, an undescribed cycadeoid is found at the north limit, latitude 54°. Whether this represents actual late extension of habitat cannot be said.

Finally, the petrified cycadeoids of India come about on the Tropic of Cancer. Whence, unless the exigencies of silicification be so great that most of the record of the heavy-stemmed cycadeoids must forever lie hidden behind the thick veil of the paleontologic past, restricted habitats are inferable, and those always with a large part of the year decidedly dry. That the cycadeoid alliance as a whole was of cosmopolitan distribution all through the Mesozoic should indicate the further capacity to live in the most varied climates, as already maintained. But that which it is especially desired to point out is that the greater silicified series of early Cretaceous time falls at a period of considerable continental emergence, in North America at least, and goes far to indicate long arid belts there covering the 35th–45th parallels, in Europe the 45th–51st. Elsewhere attention has been called to the fact that the record for Asia and Africa, likewise for South America and Australia, fails.

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[5] The Texas cycadeoid here referred to is so like the original Maryland type that it would be regarded as varietal if from the same locality. It is an isolated and thus remarkable find of Dr. Emilio Böse with whom I was associated as a paleontologist of the Instituto Geologico of Mexico during the years 1908–10. With great consideration Dr. Böse apprised me of his "find" the day it was made, in July, 1915, and later sent me the specimen. It is from the basal Trinity Beds. These rest on the Pennsylvanian, and are generally regarded as not the very oldest Cretaceous in the broader sense, but about the age of the European Aptian.

EARLY CRETACEOUS CLIMATE OF THE CYCADEOID HABITAT

In no case is it necessary to assume a Saharan heat, or even a markedly warm temperate climate, for the North American cycadeoid belt. As above pointed out, Cycadeoidea had the habitus to resist dry cold, while the associated conifer forests might well have been as able to withstand zero temperatures [–15° to –20° C.] as the Chilo-Argentine *Araucaria imbricata* forest with its lower limit undergrowth of monocarpic bamboos. Nor is it improbable that a closer scanning of the contemporaneous floras of the Lower Cretaceous "Rim" of the Black Hills as recorded from both the Morrison and Lakota, and yet destined to great extension, will compel much revision of our views of *all-tropic* Mesozoic climate. Even a brief notice of what is already known here may be illuminating.

In the 19th Annual Report of the U. S. Geological Survey, Fontaine gives an account of the plants below the Dakota—that is from the Lower Cretaceous "Rim" of the Black Hills, immediately in, above, or slightly below the great series of cycadeoids from Minnekahta and the Piedmont-Black Hawk localities. Of dicotyls there are four, called Ulmiphyllum, Ficophyllum, Quercophyllum, and Sapindopsis. Two of these occur in the Potomac of Maryland, and all are small-leaf types. It is only by a kind of elaborate argument carrying these generalized types, only known within family limits, into other zones, that they can be made to appear to have lived solely in tropic climates. And the same is true of a few species each of more or less closely associated ginkgos, conifers, and araucaroids—all small-leaf species that by themselves would easily fit into dry, to even cool climates. While three small-leaf plants of presumably cycadeoid affinity find their nearest relatives in Oregon and Greenland. Once more it is only by cumulation of disconnected inferences based on series which require much further study that these plants can be brought into the *all-tropic* scheme. Of the fern assemblage—all small of leaf—little more is known than that according to previous interpretation they easily fit the tropic category because resembling their Jurassic antecedents.

It is early to attempt a revised, well founded estimate of the full climatic significance of the Lakotan plants. This would in fact involve a further study of all Lower Cretaceous floras. Though it is evident that too much weight has been given to the superficial resemblances in extinct floras. These must always have a certain prevailing cast due to the average course of geologic change continental in magnitude. True, if a widespread tropic plant facies marks the early Mesozoic, the identical or closely related species must have a wider north-south range than later on; *but always, the similar elements of given floras, which are a reasonably sure indication of synchroneity, are only the unsafe criteria of climatic equivalence.*

A GENERAL CONCLUSION

On venturing beyond the simpler comparisons with nearly related fossil types, it becomes difficult to discuss such a highly specialized and xerophyllous plant as Cycadeoidea. There is the immense pith, the persistent armor, and the cauliflorous habit, or production of fruits along the stem below the foliage crown. The great thickness of cortical parenchyma in some forms need not be mentioned, since in some of the types with a quite heavy woody cylinder, as heavy at least as in the Cordaiteans, the pith is somewhat reduced, the cortex markedly so.

But, in the *first place*, Cycadeoidea in actuality nears certain conifers of robust form, and, where branched, finds some resemblance in Araucaria. In the tallest cycadeoid trunks, the height may be at least six times the stem diameter, exclusive of the armor of leaf bases. Now, in the Chilean *Araucaria imbricata* forest, normally grown old trees may be found with a height of only ten or twelve times the diameter of from three to six feet, while in the Sequoias of the Mariposa grove a like ratio is found in the case of various of the larger trees. For the cypress, taking the gigantic *Taxodium mucronatum* of southern Mexico, the ratio is little if any higher than in Cycadeoidea, in contrast to fifty or sixty in the taller conifers.

Secondly, the wood of *Cycadeoidea* is of a generalized type which would permit innumerable derivatives. The comparative study of tracheids suggests this, and it must be true if the complex wood ray structures of gymnosperms and angiosperms are mainly of Mesozoic origin, as the paleontologic record appears to indicate.

Thirdly, there is again full sanction in the Mesozoic record for hypothesizing progressive pith reduction all through that age, not merely in cycadeoids, but in gymnosperms generally. And with pith reduction, branching would set in, with great floral and reproductive, as well as foliar, change; though here a reverse process may also be conceived, dependent on habitat as tropic or high northern.

Fourthly, the cycadeoid floral type permitted all the sex variation possible in any flowers. The angiosperms can vary no more.

Fifthly, monocarpy which is subject to certain variations in existing plants is, in a modified, possibly in a true form, present in the cycadeoids. Great lateral series of young fruits, as well as old peduncles seen in four species afford the main evidence.

Sixthly, the cycadeoids of the silicified series are so strikingly xerophyllous that they go far to indicate vast dry to even cool belts in the mid-temperate to northern temperate zone in both Europe and America. The organization and protective features are such that light snows and some degrees of frost could have been withstood.

Seeing, therefore, that there can have been such vast change and variation in the more generalized cycadeoids, it becomes evident that there could also be notable changes in flowering as related to length of life. Hence, even to establish the presence of a pseudomonocarpy is of deep interest. If a raceme were to lengthen out its life it would become pseudomonocarpic. Evidently both mono- and pseudomonocarpy must be capable of variation with change in the length of life. And both, though in a different way, are either accompaniments of gigantism or the essential characteristic of communal forms.

EXPLANATION OF PLATES

PLATE IX

Cycadeoidea superba. A southern Black Hills trunk with five large, low subglobular branches, 75 centimeters across. Various sparsely distributed flower buds are noted, and it is quite certain that the main fruit production would have occurred later had not the initial event leading to fossilization intervened. The crowns have never been examined for the young fronds, although this form of Cycadeoidea compares most closely with the highly xerophyllous Encephalartos.

PLATE X

Portion of a slab from the Lias of the Barranca Consuelo, Oaxaca, Southern Mexico, bearing three species of Cycadeoids (?): *Otozamites Reglei* (the three complete fronds above), *Otozamites Juarezii* (large single pinnule), and *Otozamites hespera* (lower frond with narrow pinnules). Latitude 17°. These plants with the flora associated may be taken to indicate a Mexican Liassic climate much like that of today, with a probability of somewhat drier, or even of desert and cooler conditions. Slightly reduced.

PLATE XI

Cycadeoidea Dartoni. Portions of large sections traversing the many cones with the mature seeds. The dicotyledonous embryos quite fill the seed cavity, and the narrow slit separating the two cotyledons may be detected in many instances. Fig. 1 from a thin section. FIG. 2 from a polished surface. Enlarged.

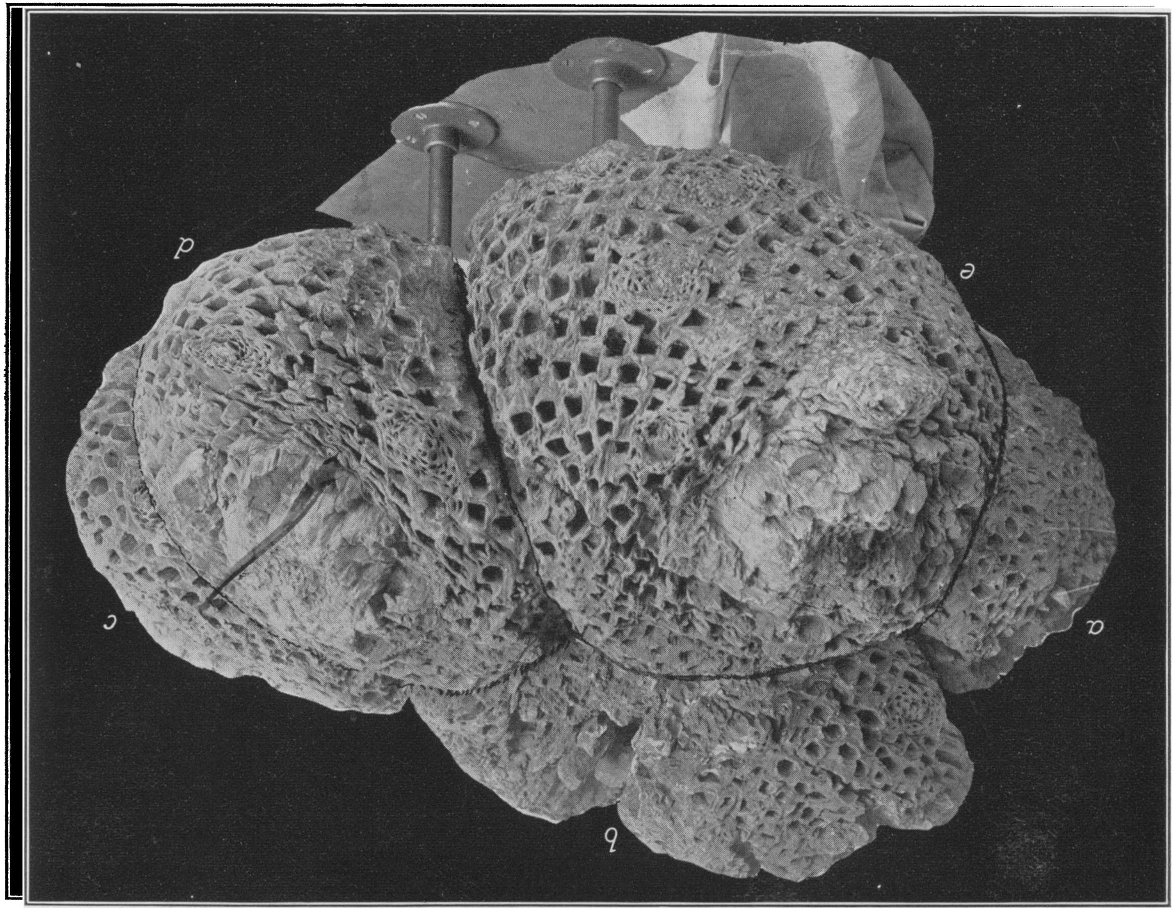
PLATE XII

FIG. 1. Transverse section through the bisporangiate strobilus of *Cycadeoidea dacotensis* showing young central cone, staminate disc (with decurved frond tips), and outer bract husk. Enlarged.

FIG. 2. *Cycadeoidea ingens.* Young non-emergent frond with folded pinnules. The most heavily haired frond type. The light dotted line of tissue is the pinnule, with a shaded band nearly as thick indicating the packed hairs. Transverse × 3.

FIG. 3. *Cycadeoidea dacotensis.* Young folded frond of the lightly haired type, but with the bases of the cutinized hairs beautifully conserved, though not showing well under about fifty diameters. Transverse × 3.

FIG. 4. *Cycadeoidea ingens.* Young folded frond with slight development of the haired feature of the pinnules. Transverse × 3.



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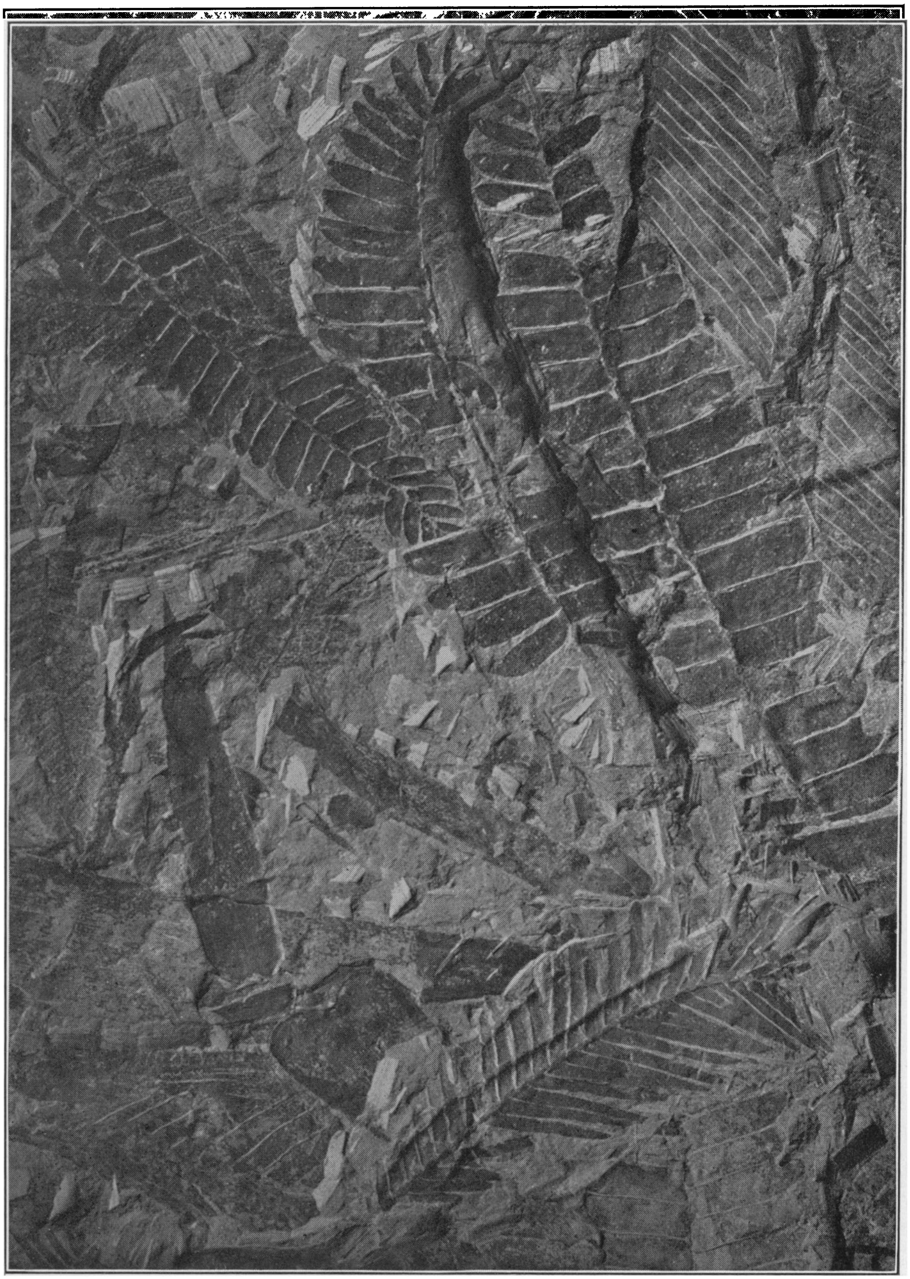

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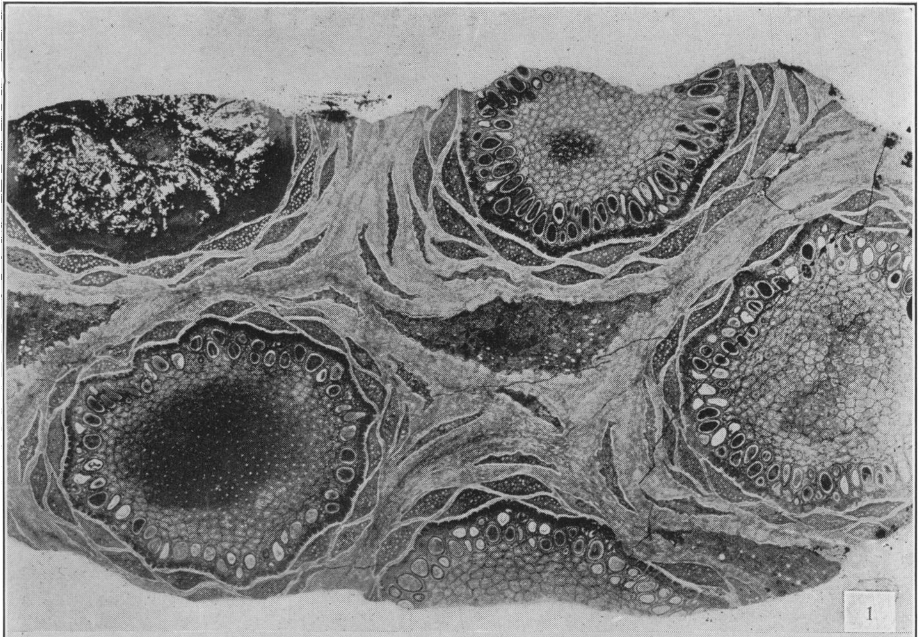

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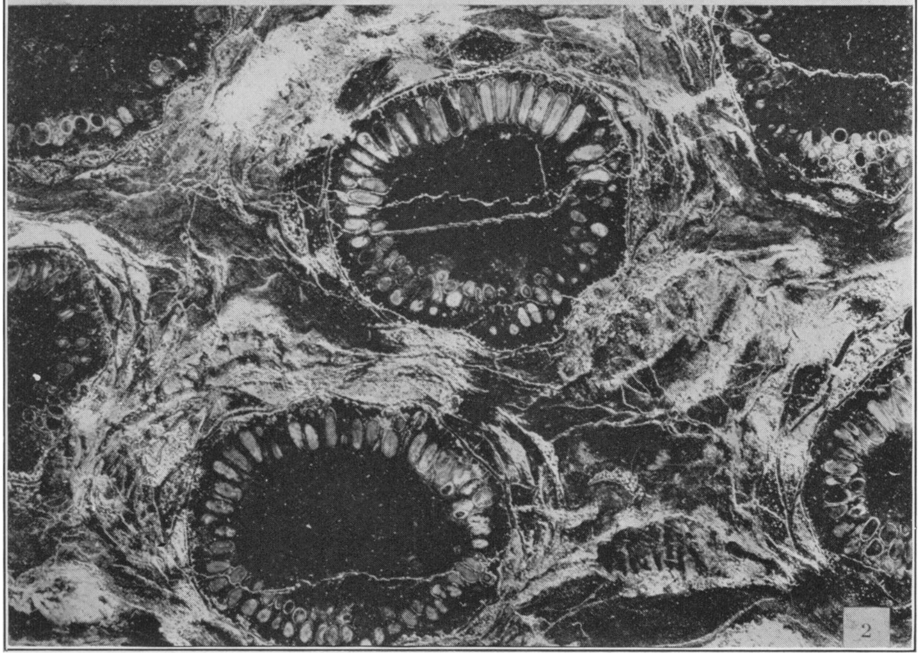

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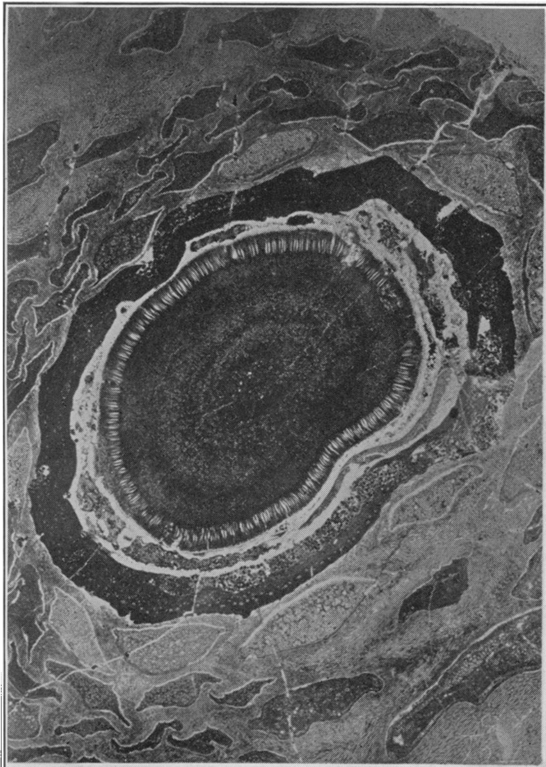

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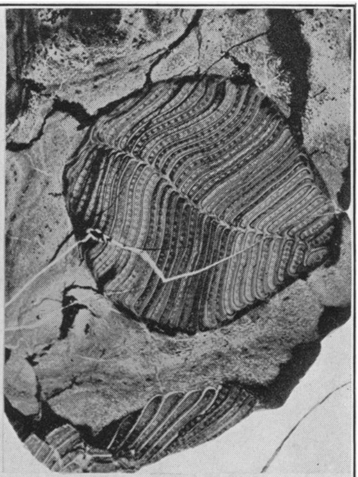

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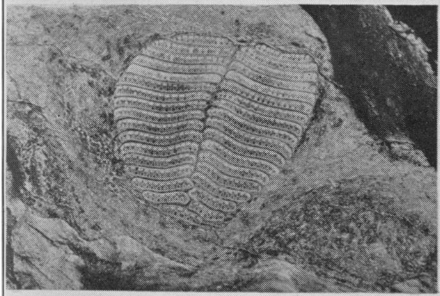

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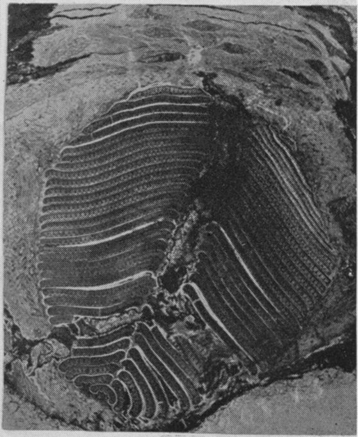

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WIELAND: CYCADEOIDS.